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Complexity within an oil palm monoculture: The effects of habitat variability and rainfall on adult dragonfly (Odonata) communities

Sarah H. Luke[1] | Andreas Dwi Advento[2] | Rory A. Dow[3,4] | Anak Agung Ketut Aryawan[2] | Holly Barclay[5] | Amy E. Eycott[1,6] | Julie K. Hinsch[1,7] | Candra Kurniawan[2] | Mohammad Naim[2] | Darren J. Mann[8] | Pujianto[2] | Dedi Purnomo[2] | Tuani Dzulfikar Siguga Rambe[2] | Eleanor M. Slade[9,10] | Soeprapto[2] | Sudharto Ps[2] | Suhardi[2] | Ribka Sionita Tarigan[2] | Resti Wahyuningsih[2] | Rudy Harto Widodo[2] | Jean-Pierre Caliman[2] | Jake L. Snaddon[11] | William A. Foster[1] | Edgar C. Turner[1]

[1]Department of Zoology, University of Cambridge, Cambridge, UK

[2]Sinar Mas Agro Resources Technology Research Institute (SMARTRI), Pekanbaru, Indonesia

[3]Naturalis Biodiversity Center, Leiden, The Netherlands

[4]Sarawak Museum Campus Project, Kuching, Malaysia

[5]School of Science, Monash University Malaysia, Selangor Darul Ehsan, Malaysia

[6]Faculty of Biosciences and Aquaculture, Nord University Steinkjer, Steinkjer, Norway

[7]Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Copenhagen, Denmark

[8]Oxford University Museum of Natural History, Oxford, UK

[9]Department of Zoology, University of Oxford, Oxford, UK

[10]Asian School of the Environment, Nanyang Technological University, Singapore, Singapore

[11]School of Geography and Environmental Science, University of Southampton, Southampton, UK

Abstract

Recent expansion of oil palm agriculture has resulted in loss of forest habitat and forest-dependent species. However, large numbers of species—particularly insects—can persist within plantations. This study focuses on Odonata (dragonflies and damselflies): a charismatic indicator taxon and a potentially valuable pest control agent. We surveyed adult Odonata populations biannually over three years within an industrial oil palm plantation in Sumatra, Indonesia. We assessed the effects of rainfall (including an El Niño Southern Oscillation-associated drought), the role of roadside ditches, and the importance of understory vegetation on Odonata populations. To assess the impacts of vegetation, we took advantage of a long-term vegetation management experiment that is part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme. We found 41 Odonata species, and communities varied between plantation core and roadside edge microhabitats, and between seasons. Abundance was significantly related to rainfall levels four months before surveys, probably indicating the importance of high water levels in roadside ditches for successful larval development. We found no significant effect of the BEFTA understory vegetation treatments on Odonata abundance, and only limited effects on community composition, suggesting that local understory vegetation structure plays a relatively unimportant role in determining communities. Our findings highlight that there are large numbers of Odonata species present within oil palm plantations and

Luke and Dwi Advento Joint first authors.

Correspondence
Sarah H. Luke, Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.
Email: sarah.h.luke@gmail.com

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suggest that their abundance could potentially be increased by maintaining or establishing waterbodies. As Odonata are predators, this could bring pest control benefits, in addition to enhancing biodiversity within intensive agricultural landscapes.

Abstract in Indonesian is available with online material.

KEYWORDS
Dragonflies, Elaeis guineensis, Indonesia, plantation management, SE Asia, sustainability, tropical agriculture

1 | INTRODUCTION

The land area used for crops has expanded rapidly across the tropics in recent decades (Laurance, Sayer, & Cassman, 2014; Phalan et al., 2013). In SE Asia, one of the most rapidly expanding crops is oil palm, which increased in area by 87 percent between 2000 and 2010 (Wilcove, Giam, Edwards, Fisher, & Koh, 2013). Indonesia is now the world's leading producer of palm oil, and annual fruit production in 2016 was over 160 million tonnes (FAO, 2018). This expansion has been achieved at the expense of natural habitat, with SE Asia experiencing 1.4 percent forest loss each year during the 1990s and 2000s (Sodhi, Koh, Brook, & Ng, 2004), resulting in almost 70 percent of forest across Sumatra, Java, and Malaysia being lost by 2010 (Wilcove et al., 2013).

Oil palm (*Elaeis guineensis*) is a perennial crop, typically grown in monoculture plantations, which are cultivated for about 25 years before replanting with another generation of palms (Corley & Tinker, 2003b). In comparison to forest, oil palm plantations are structurally simplified (Foster et al., 2011; Luskin & Potts, 2011), have hot and dry microclimates (Hardwick et al., 2015), and high levels of disturbance. For example, soils are heavily compacted and vulnerable to erosion and leaching unless protected by a cover crop (Corley & Tinker, 2003c), and there is regular use of chemical fertilizers and pesticides (Corley & Tinker, 2003a). However, compared to many other tropical crop systems, especially annuals, oil palm plantations have substantial potential to develop vegetation complexity and provide some habitat stability owing to their long lifespan, closed canopy once mature, and infrequent tillage (Wahid, Abdullah, & Henson, 2005). There is also substantial international pressure to improve palm oil (Meijaard et al., 2018), including relatively well-developed sustainability initiatives such as the Roundtable on Sustainable Palm Oil (RSPO), and Indonesian Sustainable Palm Oil (ISPO). These schemes have industry buy-in and therefore could make real management changes on the ground within plantations (Tayleur et al., 2016), although it has been widely acknowledged that improvements are still needed (Cattau, Marlier, & DeFries, 2016; Paoli, Yaap, Wells, & Sileuw, 2010; Ruysschaert & Salles, 2014).

Insects are the most numerically and functionally important animal group within most terrestrial ecosystems (Samways, 2005). A meta-analysis has shown that although persistence of forest-specialized invertebrate species is generally low in oil palm, large numbers of less-specialized species can persist. Therefore, overall invertebrate species richness in oil palm is not significantly different from primary forest (only 11% fewer species than primary forest), and certain taxa can be more diverse in oil palm (Danielsen et al., 2009). These invertebrates play important roles in delivering key ecosystem functions and services within plantations, including decomposition, soil processing, pest control, and pollination (Foster et al. 2011; Dislich et al. 2017; Li, Tscharntke, Saintes, Buchori & Grass 2019; Tao, Slade, Willis, Caliman & Snaddon 2016; Turner & Hinsch 2018; Nurdiansyah, Denmead, Clough, Wiegand & Tscharntke 2016).

Odonata are a relatively diverse and abundant invertebrate group in oil palm ecosystems in SE Asia (Abdul, Rawi, Ahmad, & Al-Shami, 2017; Dow et al., 2018; Luke, Dow, et al., 2017). Odonata (dragonflies and damselflies, henceforth referred to collectively as dragonflies) are charismatic insects that are easily visible around waterways, and also within the matrix of oil palm plantation systems. Both larval and adult Odonata are active predators and have the potential to play a role in pest control within agricultural systems (Corbet, 1980; Siregar, Rawi, Ahmad, & Nasution, 2016), including as valuable biocontrol agents for mosquito larvae (e.g., Mandal, Ghosh, Bhattacharjee, & Chandra, 2008; Saha, Aditya, Banerjee, & Saha, 2012; Sebastian, Sein, Thu, & Corbet, 1990). Their use of both freshwater and terrestrial habitats means that they are sensitive to changes in water quality and conditions within waterways to meet the needs of the larvae, as well as changes in terrestrial vegetation structure and wider habitat quality to meet the perching and foraging requirements of adults (Clausnitzer et al., 2009; Corbet, 1999; Orr, 2006). Consequently, dragonflies have been shown to be a good indicator taxon in river and wetland systems (e.g., Chovanec & Waringer, 2001; Golfieri, Hardersen, Maiolini, & Surian, 2016; Kutcher & Bried, 2014; Simaika & Samways, 2011). As an aquatic group, dragonflies are also sensitive to changes in rainfall and may therefore be affected by increasing occurrence of drought events associated with climate phenomena such as El Niño Southern Oscillation (ENSO, and hereafter shortened to El Niño and La Niña) and climate change. There has been rapid growth in research related to oil palm plantations, but only a small proportion of this has focused on biodiversity and conservation (Turner, Snaddon, Ewers, Fayle, & Foster, 2011; Turner, Snaddon, Fayle, & Foster, 2008). The

majority of studies have largely focused on comparing oil palm with natural habitats, with fewer studies that have specifically tested the effects of plantation management strategies on environmental conditions, biodiversity, or ecosystem functions (Savilaakso et al., 2014). Although recent research efforts have given more attention to the effects of possible management strategies (e.g., Ashraf et al., 2018; Azhar et al., 2015; Darras et al., 2019; Ghazali et al., 2016; Teuscher et al., 2016; Zemp et al., 2019 in a smallholder context), given the huge global coverage of the crop, there is an urgent need to further investigate management techniques that can support biodiversity within plantations without reducing yield. This is particularly the case for taxa that contribute toward important ecosystem services associated with crop production, therefore, potentially benefitting both biodiversity and yield. To date, studies of dragonflies in oil palm plantations have been very limited and have only considered the ecology of communities associated with rivers running through oil palm. Studies in Sabah found a shift in community composition of adult dragonflies and decreases in larval abundance (Luke, Dow, et al., 2017), and changes in composition of insect larvae communities in oil palm streams relative to those found in forested sites (Chellaiah & Yule, 2018). This is most likely as a result of differences in environmental conditions in rivers running through oil palm compared with those in forest, including temperature, depth, sediment, shading, width, leaf litter levels, and water nutrient levels (Chellaiah & Yule, 2017; Luke, Barclay, et al., 2017). Similar trends have been reported from oil palm streams and Odonata communities in Amazonia (Mendes, Benone, & Juen, 2019). However, beyond these broad habitat comparisons between oil palm and forest, we are not aware of any studies that have considered how Odonata populations within plantations may be affected by oil palm plantation management practices, or how any impacts might be changed by natural variation in rainfall regimes.

In this study, we conduct multiple survey rounds, across several years, in order to determine the dragonfly community present within an oil palm plantation in Sumatra, Indonesia, and environmental factors that affect their occurrence. We compare the abundance, species richness, and family-level composition of dragonfly communities within different plantation microhabitats (the core and edge of planting blocks) to assess spatial variation in communities within the plantation, and between different seasons and years to assess variation in this community over time. We consider the role of vegetation, availability of ditches, and rainfall in determining these trends.

2 | METHODS

2.1 | Site

Fieldwork was conducted within oil palm plantations in Riau Province, central Sumatra, Indonesia. The plantations are owned and managed by PT Ivo Mas Tunggal (a subsidiary company of Golden Agri Resources, GAR), with technical input from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) (the research and development center of GAR) (Figure S1). The area is naturally mixed lowland dipterocarp forest, but was deforested ~ 30 years ago, and is currently heavily dominated by oil palm agriculture, with very little non-converted habitat remaining. The region has a tropical climate, with mean annual rainfall of 2,350 mm, spread unevenly across the year, and the plantations are based on mineral soil (Tao et al. 2016).

We surveyed sites that formed part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme (Foster et al. 2014; Luke et al. 2020). As part of this, the BEFTA Understory Vegetation Project tests the effects of understory vegetation complexity on the oil palm ecosystem, through varying levels of herbicide use and manual cutting of vegetation. BEFTA has established three understory vegetation treatments (see Luke et al. 2020):

1. **Reduced complexity**: This involves spraying all understory vegetation with herbicides. Hereafter referred to as "Reduced."
2. **Normal complexity**: This is the standard practice used within the SMARTRI estates and involves an intermediate level of herbicide spraying, with harvest paths and 1.5 m circles around palms being sprayed and woody vegetation being manually removed, but other vegetation being allowed to regrow. Hereafter referred to as "Normal."
3. **Enhanced complexity**: This involves no spraying of herbicides and only limited hand-cutting of woody vegetation along harvesting paths and in palm circles. Hereafter referred to as "Enhanced."

The three treatments represent the range of different management strategies that occur within oil palm plantations. There are eighteen BEFTA Understory Vegetation Project plots, split across two estates (Ujung Tanjung and Kandista), and organized into six triplets, each at least 800 m from the next (Figure S1 and S2; Table S1). Each triplet contains one 150 × 150 m plot of each treatment, with the order allocated randomly. The middle plot in each triplet is 155 m from each of the outer plots within the triplet. Each plot is located at the end of a plantation block of 900 × 300 m, so that it is adjacent to an access road, and therefore includes both core and edge plantation microhabitat (hereafter referred to as "Core" and "Edge"). Edge sites were located alongside both a dirt road and a drainage ditch filled with standing water (Figure S2). These Edge sites occur at the end of each of the 900 × 300 m planting blocks. Core sites were within the interior of oil palm planting blocks, at least 50m from the edge. This led to differences in shading, exposure, and water occurrence in the two microhabitats, with consequent impacts on vegetation structure and diversity. Specifically, Edge areas had significantly higher plant biomass and cover, plant species richness, and higher occurrence of *Turnera ulmifolia* (planted along roadsides to promote populations of beneficial insects) than Core areas, while Core areas had significantly higher percentage cover of frond heaps (stacks of chopped palm fronds) (Luke et al. 2020; Luke, Purnomo, et al. 2019) (and also see assessments of habitat structure presented in this paper). All plots are in flat areas of the plantation, 10–30 m asl, and are in areas that were mature palm (palms planted

between 1988 and 1993) at the time of survey. The SMARTRI estates are crisscrossed by a network of small streams (Figure S1), and two plots had small streams running through them. There were no natural ponds or lakes nearby. Plots were marked out in October 2012 and were all managed using the standard SMARTRI vegetation practices (Normal complexity) until treatments began in February 2014, after which plots were managed according to their allocated understory vegetation treatment. Refer to Luke et al. 2020, for more details.

2.2 | Odonata surveying

Within each plot, adult Odonata were surveyed along transects in the Core and Edge of the plot. Core transects followed the edge of a central 50 x 50 m sampling area within each plot and so were 200 m long, while Edge transects followed the roadside edge of the plot and so were 150 m long (Figure S2). Recorders walked at a steady pace along each transect and identified and counted the dragonflies seen within a 5 m sided cube of space in front of them. Survey duration was not fixed because the time required to complete a survey depended on the number of dragonflies present. When a species was not immediately identifiable by sight, they were caught using a hand-net and photographed, allowing later identification by an experienced taxonomist (Rory A. Dow) and using identification guides (Orr, 2003; Tang, Wang, & Hämäläinen, 2010). Surveys were conducted at each plot during two "Seasons": February-April, and September, hereafter referred to as "March" and "September." Both seasons were surveyed in 2013, 2014, and 2015. Two repeat surveys of each plot were conducted within each season. Surveys conducted in March 2014 fell partly during the BEFTA Understory Vegetation Project "pre-treatment" (hereafter referred to as "pre-treatment"), and partly during the BEFTA Understory Vegetation Project post-treatment (hereafter referred to as "post-treatment") time period, and were categorized accordingly in analyses. Surveys were conducted between 9a.m. and 5p.m.

2.3 | Vegetation measurements

Vegetation measurements were taken every 10 m along each of the transects, once in March-April 2013 (pre-treatment), and again in September 2014 (post-treatment). Vegetation percentage cover (of ferns, palm fronds, bare ground, empty fruit bunch (EFB—used husks of harvested palm fruits, applied by industry as a mulch), and the non-native shrub *Turnera ulmifolia* (planted by industry along roadways to promote pest control)) was assessed by eye within a 5 × 5 m area at each point. Vegetation height was measured with a meter rule. At each measurement point, the meter rule was held in a vertical position, with its base resting on the ground, and an A4 clipboard lightly rested on the vegetation (to push down any single tall stems) and the height measured accordingly. Canopy openness was measured using a densiometer (Lemmon 1956), averaging four measurements taken North, South, East, and West at each point.

2.4 | Rainfall measurements

We recorded daily rainfall (mm) using rain gauges that each had a 100 cm^2 collecting area. Rainfall values from all rain gauges within each estate (three in Ujung Tanjung, and two in Kandista) were averaged to calculate a monthly rainfall value for each estate. In analyses, we used the estate rainfall value that was applicable to each plot. We used rainfall measures from March of the relevant year as the "monthly rainfall" value for surveys conducted during February to April, and rainfall measures from September for September surveys. In addition to "monthly rainfall," we also used the value of rainfall for the calendar month that was four months before ("rainfall four months before") the March and September dragonfly surveys in analyses. This is because dragonflies have an aquatic larval stage, and therefore presence of adults at a site is dependent on sufficient water for larval development before the survey date. Although different dragonfly species exhibit a range of reproductive strategies, the majority of tropical species are multivoltine (Corbet, 1980). The development

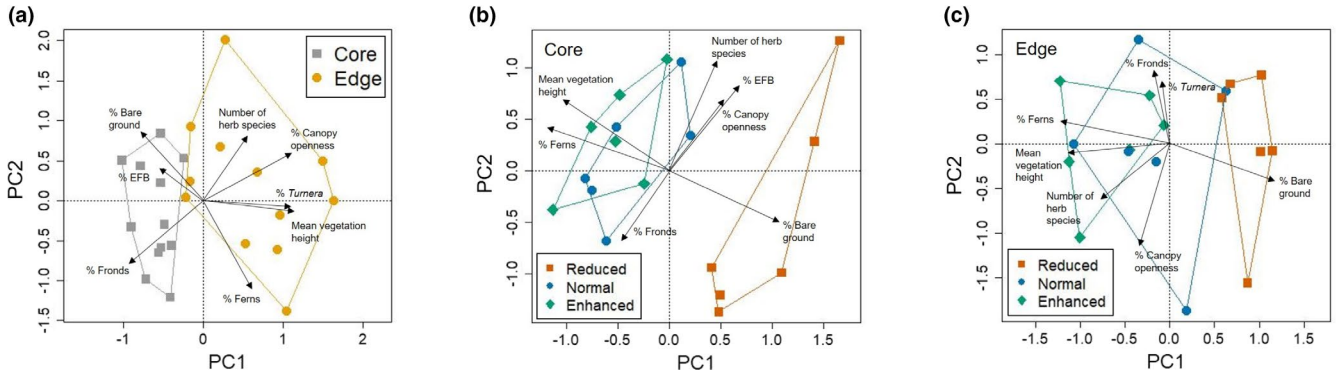

FIGURE 1 Vegetation characteristics of (a) Core and Edge habitat within Normal treatment plots, with measurements taken both pre- and post-treatment (2013 and 2014); (b) Core habitat within Reduced, Normal, and Enhanced treatment plots, with measurements taken just post-treatment (2014); and (c) Edge habitat within Reduced, Normal, and Enhanced treatment plots, with measurements taken just post-treatment (2014). In each case, points within the same habitat type are joined by convex hulls and are shown by differences in symbol and color (see individual legends). For further details of vegetation measurements refer to methods [Color figure can be viewed at wileyonlinelibrary.com]

time for many tropical dragonfly larvae is between 60 and 200 days (Corbet, 1980), the mean of which is 130 days (4.3 months). Using this lagged rainfall value in analyses allowed us to consider the influence of rainfall on egg laying, egg survival, and larval development stages of the dragonfly lifecycle, in addition to assessing impacts of rainfall on adult presence.

2.5 | Statistical analyses

We conducted analyses using R statistical program version 3.5.1 (R Core Team, 2018) and the program R Studio (R Studio Team, 2016). To compare 200 m long Core transects and 150 m long Edge transects, we standardized all abundance data to predicted values for 150 m long transects by multiplying Core abundance values by 0.75. We included data for an unidentified teneral individual ("Unknown teneral") within overall abundance models, but excluded this data point from species richness curves and family-level analyses, as its species and family were unknown.

2.5.1 | Vegetation differences within the plantation

To assess differences in vegetation between microhabitats within plots, we conducted a principal component analysis (PCA) on the Normal plot data. Data were scaled before analysis to allow fair comparisons of different variables. We compared similarity of vegetation structure between sites (Core and Edge) by plotting convex hulls (PCA conducted using "vegan" (Oksanen, 2008; Oksanen et al., 2014); plotted using base graphics). We analyzed significance of differences between Core and Edge vegetation structure using the function Adonis within "vegan" (Anderson, 2001; Oksanen, 2008; Oksanen et al., 2014) using a Euclidean dissimilarity matrix, 999 permutations, and Plot as a strata term to account for repeat measures being made within the same plots.

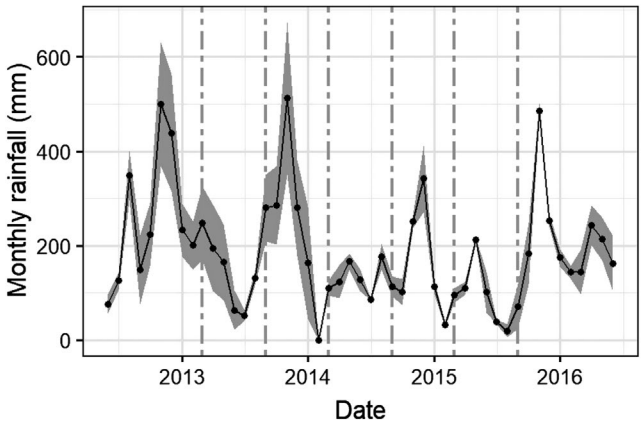

FIGURE 2 Mean monthly rainfall (mm) (±SE of the mean of Kandista and Ujung Tanjung estate values) between June 2012 and June 2016. Dragonfly sampling periods are shown by dashed gray vertical lines

We carried out PCAs (using packages as above) using only post-treatment vegetation data to assess if there were changes in vegetation structure as a result of experimental treatments. We did this separately for Core and Edge microhabitats. In both cases, we plotted the locations of sites with different treatment type (Reduced, Normal, or Enhanced) on the ordination, and joined points within the same category by convex hulls to help assess similarity of vegetation between treatment types. We also used Adonis to test significance of differences in vegetation structure between treatments (as above), with Triplet as a strata term to account for non-independence of plots within triplets.

2.5.2 | Rainfall differences over time

To assess differences in "monthly rainfall" between the two sampling seasons, we averaged the estate rainfall values for the two estates from March and September 2013–2015 (the years for which we had full rainfall data available, Figure 2) and compared the values. We also compared the March and September values in 2013, 2014, and 2015 to consider if there were differences in rainfall during sampling times between different years. We then repeated both comparisons using "rainfall four months before."

2.5.3 | Effects of vegetation and rainfall on dragonfly populations

We plotted differences in dragonfly abundance (using the package "ggplot2" (Wickham, 2009)), constructed species accumulation curves (using the package "iNEXT" (Hsieh, Ma, & Chao, 2014)), and carried out Non-metric Multidimensional Scaling (NMDS) analysis using family-level data (with "vegan" (Oksanen, 2008; Oksanen et al., 2014); plotted using base graphics) to visualize differences in dragonfly communities between microhabitats (Core and Edge), seasons (March and September), and years (2013–2015). We tested for significant differences in family-level community composition between microhabitats, seasons, and years using ANOSIM with a Bray–Curtis dissimilarity matrix, 999 permutations, and Plot as a strata term to account for repeat measures being made within the same plots (function "anosim" (Clarke, 1993), within "vegan" (Oksanen, 2008; Oksanen et al., 2014)). To assess the relative importance of the variables driving these differences, we used linear mixed-effects models (lmer, "lme4", (Bates, Mächler, Bolker, & Walker, 2015)) with a Gaussian error structure. We ran models using abundance of the full assemblage as the response, and included microhabitat type (Core or Edge), a measure of rainfall, and the interaction of microhabitat and rainfall as fixed effects. We included plot as a random effect to allow for repeat measures being made at the same plots. We used only data from the Normal treatment plots to avoid any influence of experimental treatment, and log10(value + 1) transformed abundance data to meet assumptions of homoscedasticity and normality of residuals. We used log-likelihood ratio tests with reduced and null models to assess significance of fixed effects. We first ran models with

"monthly rainfall" as the rainfall measure, and then ran models using "rainfall four months before." Refer to Table S2 for further details of the analyses conducted.

To assess whether understory vegetation experimental treatment had an effect on dragonfly abundance, we conducted linear mixed-effects models (lmer, "lme4", (Bates et al., 2015)) as described above. We used the full pre- and post-treatment data set, but split this into separate analyses for Core and Edge microhabitats. Understory vegetation treatment (Reduced, Normal, or Enhanced) and pre-/post-treatment time period were included as fixed effects, with the interaction between them serving as an indicator of a significant experimental effect. We included "rainfall four months before" and "Plot" as random effects. As above, models were run using logged abundance of the full assemblage as the response. We plotted species richness curves and family-level NMDS diagrams, and conducted ANOSIM analyses (using the methods and packages described above, but with Triplet as a strata term) using only the post-treatment data in order to assess differences in species numbers and dragonfly community between experimental treatments. Refer to Table S2 for further details of the analyses conducted.

3 | RESULTS

3.1 | The overall dragonfly assemblage within the plantation

We observed a total of 5312 dragonflies, from 41 different species within 7 different families (Aeshnidae, Gomphidae, Libellulidae, Platycnemididae, Lestidae, Chlorocyphidae, Coenagrionidae). The majority of individuals (3681) were *Neurothemis fluctuans*, and we recorded > 100 individuals from six further species (*Gynacantha dohrni*, *Lathrecista asiatica*, *Orthetrum chrysis*, *Pseudocopera ciliata*, *Archibasis viola*, and *Ceriagrion cerinorubellum*). Sixteen species were each represented by fewer than 10 individuals, with four species observed only once during the entire study (*Cratilla metallica*, *Nesoxenia lineata*, *Agriocnemis femina*, and *Pseudagrion pruinosum*) (Table S3). The Odonata community consisted mainly of widespread eurytopic species and may be similar to what might be expected from the edge or large clearings of lowland forest. We did not find any species that were endemic to Sumatra, but, owing to limited study of the Odonata assemblages within Sumatra, it is difficult to assess how this result compares with background levels of endemicity.

3.2 | Vegetation differences within the plantation

Core and Edge microhabitats had significantly different vegetation structure (Adonis: $F = 8.86$, $df = 1$, $R^2 = 0.29$, $p = .001$). Over 65 percent of the variation in vegetation within Normal plots was summarized by the first two principal components of the PCA, with Core microhabitats being characterized by high percentage cover of bare ground, empty fruit bunches (EFB), and dead palm fronds (Figure 1a), whereas Edge microhabitats had higher numbers of herb species, higher canopy openness, higher average vegetation height, more ferns, and also *Turnera* beneficial plants (Figure 1a).

Manipulation of herbicide use and manual cutting as part of the BEFTA Understory Vegetation Project had significant impacts on understory vegetation structure within both Core and Edge areas (Adonis: Edge $F = 3.34$, $df = 2$, $p = .002$; Core $F = 4.31$, $df = 2$, $p = .004$). Over 70 percent of variation in vegetation structure between Core habitats within Reduced, Normal, and Enhanced understory vegetation plots was explained by the first two principal components in PCA. The key features of Core areas in Normal and Enhanced plots were their high percentage cover of ferns and high average vegetation height, whilst Reduced plots were dominated by bare ground (Figure 1b). Other vegetation characteristics (including percentage cover of fronds and EFB, percentage canopy openness, and number of herb species) were not strongly associated with any of the three treatment types (Figure 1b). In Edge habitats, 66.3 percent of the variation in vegetation structure across treatments was explained by the first two components of the PCA. There was a less substantial difference between Edge habitats in Reduced, Normal, and Enhanced plots, but nevertheless, Edge areas in Reduced plots were dominated by bare ground, while Normal and Enhanced plot Edge areas comprised a greater mix of ferns, frond piles, *Turnera* beneficial plants, and other herbs, and had higher vegetation height and greater canopy openness (Figure 1c).

3.3 | Rainfall differences over time

There was substantial variation in rainfall between months and years (Figure 2). Although average rainfall levels were similar in March and September (the months when dragonflies were sampled) (151 mm cf. 155 mm), average rainfall across the March and September sampling months was higher in 2013 than in 2014 and 2015 (264 mm cf. 112 mm cf. 84 mm) (Figure 2). When considering "rainfall four months before," there were much more pronounced differences in average levels for March and September, with rainfall levels four months before the March collection period being an average of 421 mm, compared to 181 mm for September (Figure 2). There were also differences across calendar years, with the average of "rainfall four month before" the March and September sampling months being lower in 2015 than in 2013 and 2014 (232 mm *cf.* 333 mm *cf.* 340 mm) (Figure 2).

3.4 | Effects of vegetation and rainfall on dragonfly populations

Edge habitats had higher dragonfly abundance than Core habitats (Figure 3a). Species richness estimates appear marginally higher in Core habitat compared with Edge (Figure 3b), although sample completeness was lower in Core than in Edge habitat, making it

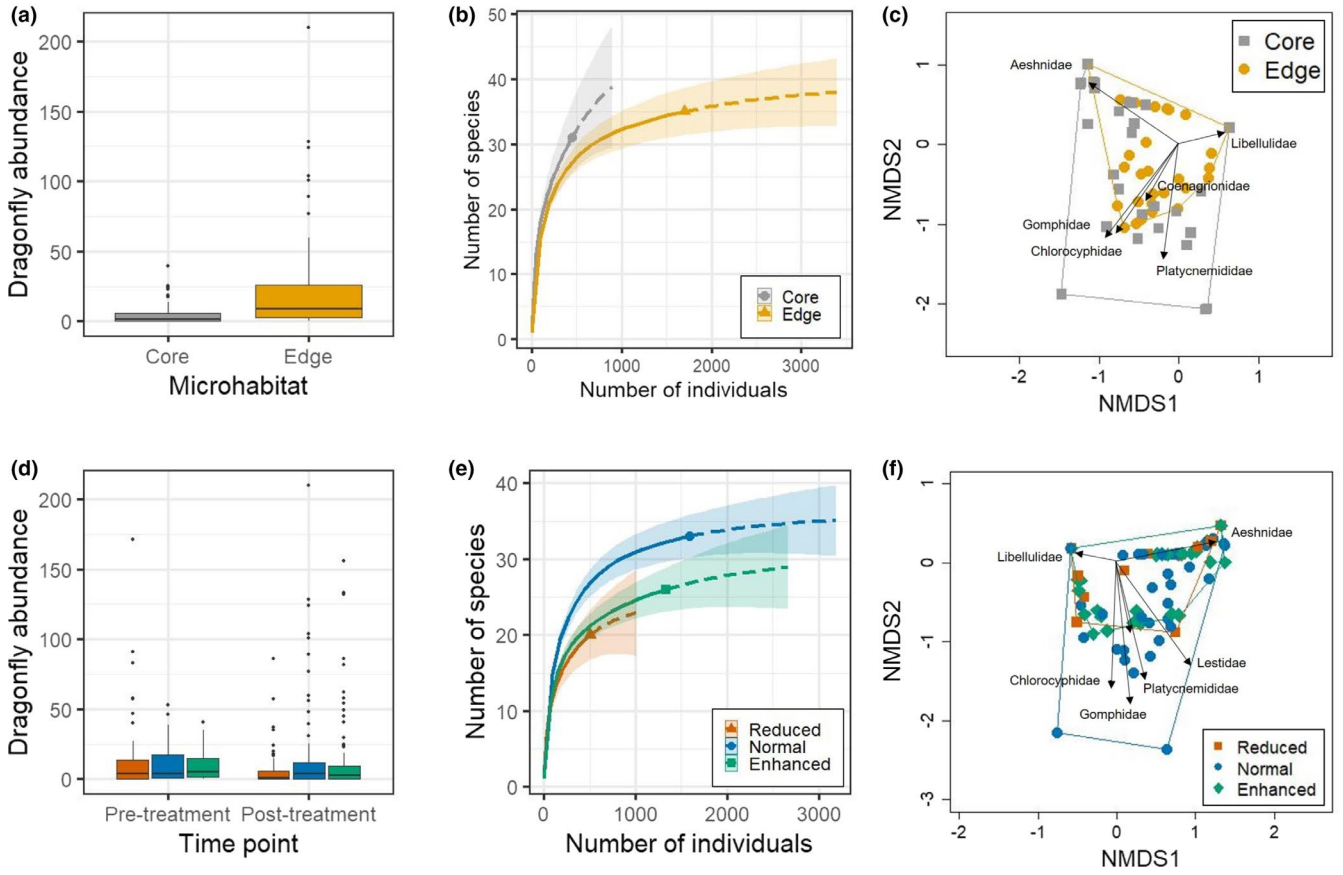

FIGURE 3 Dragonfly abundance (mean per 150 m length of transect); interpolated and extrapolated numbers of dragonfly species present; and family-level community composition in Core and Edge habitats (a-c); and within plots with different understory vegetation treatments (Reduced, Normal, and Enhanced) (d-f). Figures (a-c) are based on data from Normal plots, and figures (d-f) are based on post-treatment data. Data for the boxplots and ordinations are scaled to a 150 m long transect so that Core and Edge results can be compared fairly. In the ordinations, grouped plots are joined by convex hulls, and arrows and labels indicate occurrence of dragonfly families. Refer to individual legends within panels for details of symbols and colors used [Color figure can be viewed at wileyonlinelibrary.com]

difficult to be certain of estimates. Family-level community composition varied between Core and Edge microhabitats, with the families Libellulidae and Coenagrionidae dominating Edge sites, and Gomphidae, Chlorocyphidae, and Platycnemididae more likely to be found in Core sites (Figure 3c). There were significant differences in the family-level assemblage of Core and Edge sites (ANOSIM: $R = 0.154$, $p = .001$).

We found no significant effect of manipulating understory vegetation levels on overall abundance of dragonflies within plots as a whole ($X^2 = 0.478$, $df = 2$, $p = .787$) (Figure 3d), or in either Core habitat ($X^2 = 4.874$, $df = 2$, $p = .087$), or in Edge habitat specifically ($X^2 = 0.387$, $df = 2$, $p = .824$) (Figure S3a,b). Species richness estimates across plots as a whole neared asymptote, and appear similar in Reduced, Normal, and Enhanced understory vegetation plots (Figure 3e). When looking at Core microhabitats specifically, estimates of species richness appear substantially lower in Reduced vegetation plots compared with Normal and Enhanced (Figure S3c); however, confidence intervals on these estimates are large. Our data from Edge habitats allow more certain estimates of species richness and suggest that richness is higher in the Edge habitat of Normal plots than in Reduced or Enhanced (Figure S3d). Family-level community composition within the plots as a whole appeared fairly homogenous, but some Normal plots had a greater range of families, which led to an overall significant difference in family-level community composition between treatments (ANOSIM: $R = 0.026$, $p = .012$) (Figure 3f). When we looked at Core and Edge assemblages separately we found significant differences between treatments within Core habitat (ANOSIM: $R = 0.075$, $p = .001$), with Reduced plot Core assemblages being the least diverse, and Normal Core assemblages the most varied (Figure S3e). There were no significant differences in Edge assemblages across understory vegetation treatments (ANOSIM: $R = -0.008$, $p = .597$) (Figure S3f).

Dragonfly abundance was higher in March than in September (Figure 4a). Species richness estimates were marginally higher in September compared with March (Figure 4b), but the differences are not substantial. The dragonfly assemblages caught in March and September were different at the family level (ANOSIM: $R = 0.054$, $p = .016$), with the community caught in March surveys appearing to be slightly more homogenous than that caught in September (Figure 4c). There were no substantial differences in abundance between sampling years (Figure 4d). Species richness estimates were also similar across years (Figure 4e). Community composition

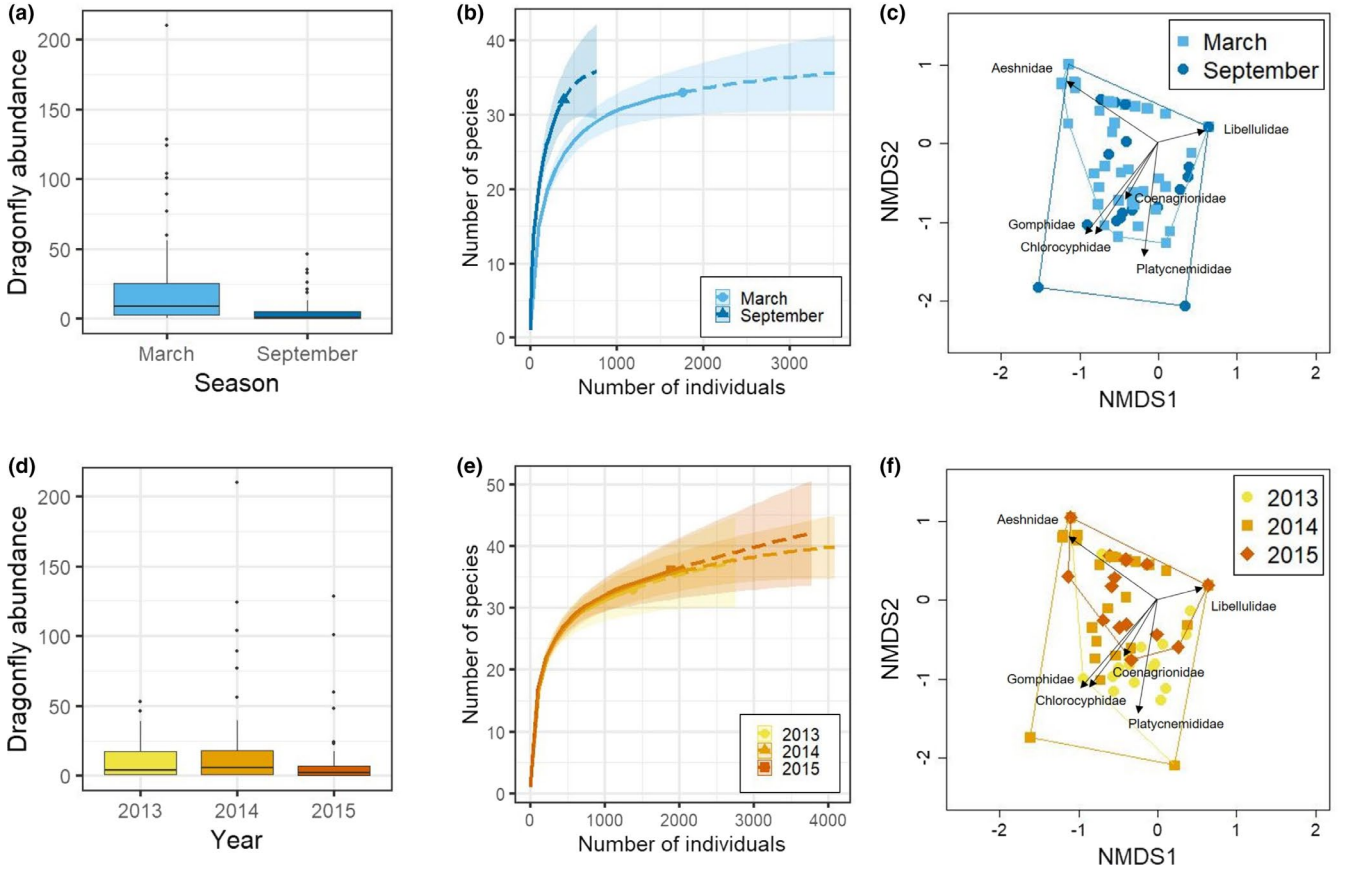

FIGURE 4 Dragonfly abundance (mean per 150 m length of transect); interpolated and extrapolated numbers of dragonfly species present; and family-level community composition in March and September (a-c); and different years (d-f). All figures are based on data from Normal plots, and for the boxplots and ordinations are scaled to a 150 m long transect so that Core and Edge results can be compared fairly. In the ordinations, grouped plots are joined by convex hulls, and arrows and labels indicate occurrence of dragonfly families. Refer to individual legends within panels for details of symbols and colors used [Color figure can be viewed at wileyonlinelibrary.com]

showed some shifts year by year (Figure 4f), but differences were not significant (ANOSIM: $R = 0.014$, $p = .089$).

Normal plantation management techniques were not changed during the course of the study, and so the temporal differences that were observed in dragonfly communities were likely to be related to differences in rainfall (Figure 2). Considering this in combination with the effect of varying microhabitat (Core or Edge) allowed us to model the variation in dragonfly abundance seen across space and time within the plantation. When we included monthly rainfall (rainfall at the time of sampling) in the model alongside microhabitat, we found a significant effect of microhabitat, with Edge habitats showing higher dragonfly abundance than Core habitats, but no effect of rainfall (Figure 5a,c). This therefore explained some of the variation in Core and Edge habitats that we observed (Figure 3a), but not the additional differences observed across seasons, or years (Figure 4a,d). However, when we used rainfall levels four months before the time of sampling we found a highly significant effect of rainfall on dragonfly abundance, and also a significant interaction between rainfall and microhabitat—with the association between rainfall and abundance being much stronger within Edge than in Core habitat (Figure 5b,c)—which together explain the differences observed between Core and Edge habitats across seasons, and years (Figure 4a,d).

4 | DISCUSSION

4.1 | The overall dragonfly assemblage within the plantation

In this study, by means of repeat sampling over an extended period, we have been able to establish that oil palm plantations can contain a diverse and abundant population of dragonflies: 41 species from 7 families. This is almost half of the known species from Riau Province, Sumatra (i.e., 88 species from 12 families, (Dow et al., 2018)). Although it must be acknowledged that the region is poorly studied, and also that none of the species observed in our study were Sumatra endemics, the community found within the plantation is nevertheless a relatively rich and potentially important assemblage of these charismatic animals. As we did not survey riverine areas within our study, this community represents what is likely to be present across large areas of plantations, but also suggests that additional species could well be present over the wider landscape if river and stream communities were fully investigated. The assemblage was dominated by Libellulidae (22 species, ca 83% of individuals) and Coenagrionidae (10 species, ca 7% of individuals), which are typical of non-forest habitats (Orr, 2006). However, it

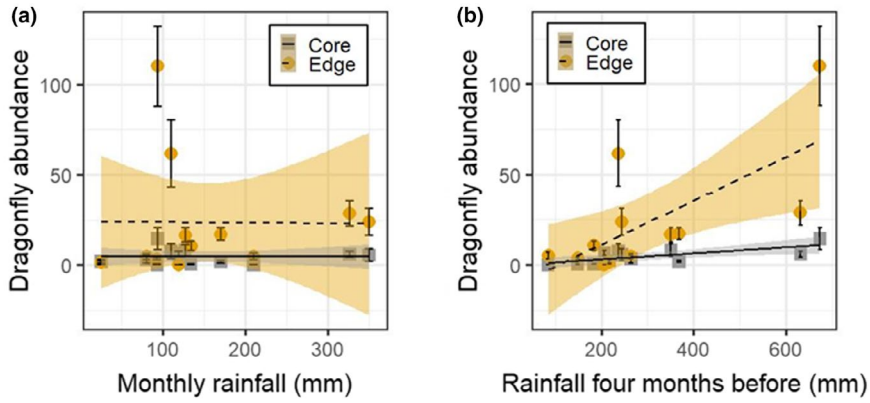

FIGURE 5 Relationship between dragonfly abundance (mean per 150 m length of transect within Normal plots) and rainfall within that sampling month ("monthly rainfall") (mm) (a); and with rainfall four months before the sampling month ("rainfall four months before") (mm) (b). Different symbols and colors are used to show Core and Edge results (refer to legends), and the relationships between rainfall and dragonfly abundance are indicated using lm smoothers and are shown separately for Core and Edge (refer to legends for details of line type). Results of linear mixed-effects models to test the significance of the relationships between dragonfly abundance, and habitat (Core or Edge), rainfall, and the interaction effect of habitat and rainfall are shown in (c) [Color figure can be viewed at wileyonlinelibrary.com]

(c)

	Monthly rainfall model			Rainfall four months before model		
	X^2	*df*	*p*	X^2	*df*	*p*
Habitat*Rainfall	2.628	1	0.105	4.825	1	0.028
Rainfall	0.256	1	0.613	42.953	1	<0.001
Habitat	31.424	1	<0.001	40.625	1	<0.001

also included at least 15 species considered to be forest dependent (requiring the presence of forest for their survival), while at least 22 fall clearly into the non-forest-dependent category (Orr, 2005, 2006). Two species recorded from the plots breed only in running water (*Libellago hyalina* and *Prodasineura collaris*) (Orr, 2005) and were predominately found close to small streams that ran through our plots. As far as we are aware, this is the first study to investigate dragonfly populations within an industrial oil palm matrix, away from river habitats, and to show that plantations can provide valuable habitat for this taxon.

4.2 | Key factors determining dragonfly communities

Edge habitats had higher dragonfly abundance than Core habitats, which we infer was caused by the effects of rainfall (specifically "rainfall four months before sampling") and the presence of ditches in Edge areas. The importance of rainfall is also indicated by the higher levels of dragonfly abundance in March (after the rainy season) than in September (after a drier period). The Edge habitats all contain ditches, which fill up with water during the rainy season, potentially providing suitable habitats for larval dragonflies. These ditches are not present within the Core habitats. Although the BEFTA Understory Vegetation Project caused substantial changes in vegetation structure, particularly within Core habitat, we found no significant effect of treatment on dragonfly abundance in the first 1.5 years post-treatment that are considered in this study. Species richness estimates suggested no substantial differences in relation to microhabitat or rainfall, and although community composition was variable over space and time and we found evidence of less diverse assemblages within the Core areas of Reduced understory vegetation plots, there was not a clear turnover of assemblage between treatments.

The ditches beside the Edge habitat are filled with standing water throughout the year, apart from during the driest periods. There are no ponds, and only limited numbers of streams and rivers within the wider landscape. As dragonflies have an aquatic larval stage, it is likely that the ditches therefore provide valuable habitat for a range of species. In particular, the Libellulidae and Coenagrionidae families, which were especially abundant in Edge habitats, include many species that use shallow, standing water for egg laying and larval development (Orr, 2005). Adults may be found in particularly high numbers near water because they may be egg laying or mate guarding while a female is laying, defending a territory, or may have just emerged (Corbet, 1980, 1999). Dragonflies are found in and around ditches and roadside ponds in temperate agricultural systems (Chester & Robson, 2013; Herzon & Helenius, 2008) and have been found in high abundance in rice paddy fields in India (Mondal & Dwari, 2017; Rohmare, Rathod, & Parasharya, 2016), but studies within the matrix of other tropical crops are currently lacking.

The dependence of dragonflies on water for egg hatching and larval development, and the use of temporary water bodies including shallow roadside ditches, means that the dragonfly assemblage within the plantation is likely to be highly affected by changes in rainfall. Indeed, our results suggest that there were peaks in the adult dragonfly numbers within Edge habitats four months after high rainfall levels, which is the approximate average development time for the larvae of many tropical species (Corbet, 1980). This suggests that either egg-laying rates are higher, egg survival or early larval

survival rates are higher during periods of high rainfall, or indeed, a combination of these variables is occurring. A study of dragonfly larvae in rice fields in Malaysia found that presence of water was the most important factor for determining larval abundance. It was found that populations built up within a few days after inundation, suggesting that adults were relatively long-lived and were egg laying constantly, but that water levels then determined egg survival (Che Salmah, Hassan, Abu Hassan, & Ali, 1998). Restricted water supplies within their tree-hole habitat resulted in cannibalism among larvae of a damselfly in Panama, indicating that population levels may become reduced at the larval stage when water is scarce in this system. Later-generation larvae also died when tree holes dried out fully during the dry season (Fincke, 1994). Although wet seasons are beneficial for egg and larval stages, adult dragonflies have been found to have reduced life expectancy during rainy periods within the tropics (Palacino-Rodriguez, Contreras-Sanchez, & Córdoba-Aguilar, 2012), potentially confounding some of these effects.

The strong link between Edge dragonfly abundance and rainfall suggests that dragonfly communities could be severely affected by a prolonged period of drought or conversely, by a period of high rainfall, such as those associated with an El Niño or La Niña event, or induced by climate change. Apart from six species that were only caught in Edge habitats (*Cratilla metallica*, *Nesoxenia lineata*, *Agriocnemis femina*, *Ceriagrion auranticum*, *Pseudagrion pruinosum*, *Pseudagrion rubriceps*) but in very low numbers, and a single species (*Agrionoptera sexlineata*) that was caught only in Core habitat, the same species were found in both habitats, suggesting that presence of water largely affects the relative abundance of species, or the time spent out in the open defending territories, rather than their absolute presence or absence. The high numbers seen at Edge sites four months after rains are therefore not a unique assemblage, but rather represent a boom in the population of ditch- and open-habitat associated species. Population cycles could have substantial impacts on the ability of dragonflies to provide pest control services, as they may only be able to exert a noticeable control on pest numbers when in high numbers and when adults are aggregated (Corbet, 1980).

In addition to a dependence on aquatic habitats, adult dragonflies use vegetation for perching, and often choose to forage in vegetated areas (Clausnitzer et al., 2009; Corbet, 1980; Orr, 2006), and so could potentially be affected by changes in understory vegetation structure. Indeed, other studies have found that dragonfly community composition changed in response to loss of vegetation (da Silva Monteiro Júnior, Couceiro, Hamada, & Juen, 2013), and that presence of more varied vegetation within restored wetlands supported a broader dragonfly assemblage (Mabry & Dettman, 2010). However, although there were significant differences in understory vegetation structure between Core and Edge habitat, and between Reduced, Normal, and Enhanced plots, we found no significant effects of the BEFTA Understory Vegetation Project on dragonfly abundance. We did, however, find evidence for changes in community composition within Core areas of treatment plots, with more limited diversity in Reduced plots, and the greatest diversity within Normal plots, but Enhanced plots providing no apparent additional benefit. Together, this suggests that understory vegetation structure may have some effect on dragonfly communities but—at least within the range of management treatments normally experienced within plantations—was not the most important factor driving the persistence of most species. This lack of difference may be related to the substantial structural complexity that is present in even Reduced treatments, such as numerous cut palm fronds and the oil palms themselves. The result could also be related to the high dispersal ability of dragonflies. Although the plots used in this study were large, it is likely that dragonflies were still moving in from surrounding areas, reducing the effect of understory treatment.

A final factor that may have contributed to the differences in dragonfly communities between Core and Edge habitats was the extent of canopy openness. Edge habitats generally had a much more open canopy than Core habitats because they were beside roads. Habitat selection by adult dragonflies is heavily affected by degree of shading (Clausnitzer et al., 2009; Oppel, 2005; Remsburg, Olson, & Samways, 2008). Many of the species within the assemblage were sun-loving Anisopterans, and historically would have only reached high abundances in open, forest-clearing areas (Orr, 2006). Shade-loving, forest-dependent species (Orr, 2005, 2006) were less represented within the assemblage in our plantation. They did not even appear in very high numbers within the comparatively shaded Core areas, and we did not find any species that require tall, intact canopy (Rory A. Dow personal observation), suggesting that oil palm plantations are not able to support high numbers of forest-dependent species.

4.3 | Management implications

This study demonstrates that oil palm plantations can support a diverse assemblage of dragonflies, and that there is heterogeneity in this community over space and time, most likely as a result of presence of water bodies, differences in canopy openness, and changes in rainfall. Differences in understory vegetation structure appeared to have relatively limited effects on dragonfly communities, indicating that adjusting herbicide use and cutting regimes would do little to increase the overall population, at least at the scale and over the timeframe of this study. However, as dragonflies can move considerable distances, it is possible that this result is dependent on this study being based within a plantation that contains reasonable levels of vegetation structure over a large area, potentially supporting high dragonfly numbers at the landscape scale. Adult dragonflies were found in highest numbers in the edge areas, where ditches were present, and we found a significant correlation between adult dragonfly abundance and rainfall levels, most probably through its effect of maintaining larval habitat. This suggests that active management of water bodies within plantations, including regular clearance of debris and vegetation to help maintain depth during drought periods, as well as creation of additional ditches and ponds within the landscape, could boost populations. Increasing dragonfly populations would not only help to increase overall biodiversity levels within the plantation,

but—owing to their showiness—would be a highly visible sign of good plantation health. In addition, as there is the potential that they could contribute to pest control, managing plantations to support healthy dragonfly populations may also bring benefits for yield, while their role in consuming mosquito larvae, could also bring health benefits to plantation staff, through control of potential disease vectors.

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CONFLICT OF INTEREST

Co-authors listed with a Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) affiliation were employed by SMARTRI, the research division of Golden Agri Resources (GAR), at the time of the study. The BEFTA Programme is co-funded by GAR. However, there is an MOU in place that protects the intellectual freedom and data-use for all researchers working on the project. The Programme therefore represents a collaboration between the University of Cambridge and an oil palm company, ensuring that results are readily disseminated to inform best management practices, but maintaining academic independence.

AUTHOR CONTRIBUTION

ET, WF, SP, JS, and J-PC designed the manipulation experiment, and ADA, AAKA, CK, MN, P, DP, SP, TR, Su, RT, RHW, RW, and J-PC maintained it. ET, ADA, HB, WF, DM, DP, ES, JS and So designed survey protocols. ADA led the data collection, with assistance from DP, So, AE, and JH. Identifications were verified by RD. SL performed the data analysis and wrote the manuscript. All authors commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.00000 (Luke, Advento, et al., 2019).

ORCID

Sarah H. Luke https://orcid.org/0000-0002-8335-5960
Andreas Dwi Advento https://orcid.org/0000-0002-2208-7376
Holly Barclay https://orcid.org/0000-0002-0027-2570
Amy E. Eycott http://orcid.org/0000-0002-8609-1091
Julie K. Hinsch https://orcid.org/0000-0001-5533-5615
Darren J. Mann https://orcid.org/0000-0002-6732-6940
Tuani Dzulfikar Siguga Rambe https://orcid.org/0000-0001-6287-9338
Eleanor M. Slade http://orcid.org/0000-0002-6108-1196
Jake L. Snaddon https://orcid.org/0000-0003-3549-5472
William A. Foster http://orcid.org/0000-0002-2535-8012
Edgar C. Turner https://orcid.org/0000-0003-2715-2234

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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